

SPACE USE AND MOVEMENTS OF MOOSE HUNTERS AND WOLVES IN

THE YUKON FLATS, ALASKA


By


Ian Johnson

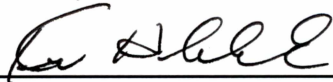
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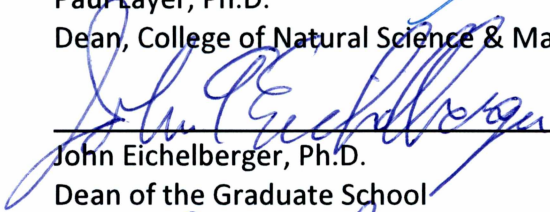

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SPACE USE AND MOVEMENTS OF MOOSE HUNTERS AND WOLVES IN
THE YUKON FLATS, ALASKA

A
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Abstract

Within the Yukon Flats, Alaska, subsistence communities utilize moose (*Alces alces*) as a primary resource (78% of households) and wolves (*Canis lupus*) hunt them as an obligatory prey item. Hence, understanding the potential of direct or indirect competition between wolves and humans is useful for managers.

In Chapter 1, I used a novel approach utilizing spatially-linked interviews to quantify the distance subsistence users were traveling from communities and rivers to harvest moose in the Yukon Flats. My study was the first to quantify hunter access in the Arctic and may provide managers with a harvest estimation approach that may supplement the current harvest ticket system, for which reporting is considered consistently low. My final results and model may be used by game managers outside of the Yukon Flats where hunter success is linked to access to forecast the impact of creating new access on game populations or forecast the effect of access closure on game populations.

In Chapter 2, I quantified wolf movement and evaluated resource selection by wolves within a low prey-density system. I used Global Positioning System (GPS) collars to characterize wolf movement. My results were the first in the literature to examine wolf movements in a low prey-density system and demonstrate that wolves travel farther to make kills. My results provided a mechanism for explaining large wolf territories, which are documented in low prey-density systems, and in our system. Within high prey-density systems, managers could expect wolf travel distances to increase if prey density decreases, resulting in larger territories within

their respective systems. My results also demonstrate that similar to high prey-density systems, wolves were utilizing river corridors.

By understanding that hunter access for moose and wolf travel paths both occur along rivers, we postulate possible competition along navigable waters. I used the results of my spatial analysis in Chapter 1 and Chapter 2 to evaluate the likelihood of competition between hunters and wolves. I found that in a pack overlapping navigable water, 75% of its use points fall within hunter use areas. However, my spatial data of wolf and human use did not overlap temporally. I suggest that evaluating competition would require comprehensive biological and social datasets which encapsulate moose, wolf, and human behavior. It is critical that these dataset overlap spatially and temporally.

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Preface

I cannot thank enough my parents for raising me as they did. It is very hard to imagine being in my current shoes without a school of natural science and life lessons out my back door in the Midwest. Their influence has shaped me to be driven, and to achieve what I set out to do. A huge thanks, and, “I love you!” to my fiancé, who has put up with my meddlings in Alaska, Maine, and Wisconsin and shown nothing but support.

From a professional development side, a monstrous thanks to my advisor, Todd Brinkman. I did not realize how green behind the ears I was until he put my thesis drafts through their paces, showing endless patience. Thank-you to my committee, I have opted to format the results in a collaborative tense; it does not seem right to use “my results,” when “our results” captures the context that you have helped me place them in.

Thank-you to my Co-advisor Kris Hundertmark for helping frame my research questions and reviewing my drafts. Thanks to my committee members David Verbyla and Bryce Lake for providing useful insight and context to my results. Thanks to Kelda Britton and James Kelly from the Council of Athabascan Tribal Governments for providing a data-sharing agreement and reviewing the results of this work to ensure they were applicable to the community members. Thank you to hunters who participated in this study. Thank-you to my funding sources including the Resilience and Adaptation Program, Bureau of Land Management, Council of Athabascan Tribal Governments, Alaska EPSCOR, Alaska Trappers Association, the Department of Biology and Wildlife, and the University of Alaska Fairbanks Graduate School.

Introduction

Effective wildlife management requires knowledge of the interactions among wildlife, habitat, and humans. Since the profession of wildlife management was established in the 1930s (Leopold, 1933) most wildlife research has focused on wildlife population dynamics and the interactions of wildlife and habitat (Hirst, 1975; Morrison, Marcot, & Mannan, 2006; Rempel, Elkie, Rodgers & Gluck, 1997). Over time, Leopold's (1933) definition of wildlife as "crops" of deer (*Cervidae*), ducks (*Anatidae*), and other game animals has changed in many ways, including encompassing non-game species. In its current broader definition, wildlife researchers collect information to inform game harvest levels (Schwartz, Hundertmark, & Spraker, 1992), identify important areas for conservation (Laurance & Yensen, 1991), control invasive species (Carlton & Ruiz, 2003), or research human use of the environment (Brinkman et al., 2014).

In the last 20 years, the role of humans within wildlife management systems has received more attention. This recent science-based branch has been labeled the human dimensions of wildlife (HDW) management (Decker & Chase, 1997; Decker, Riley, & Siemer, 2012). Human dimension practitioners assert that traditional biological techniques are important for wildlife management, but so are methods related to managing interactions of people and wildlife (Decker & Richmond, 1995). As such, we generally define HDW as determining what people think and do when interfacing with wildlife. In the context of wildlife management, it guides decision-making, implements practices, and influences interactions between people but also between people, wildlife, and wildlife habitat with the goal of addressing stakeholder needs (Decker & Lipscomb, 1991; Decker et al., 2012).

Traditionally, HDW research has borrowed theories and methodologies from the social sciences in the disciplines of social psychology, sociology, or economics. These give insights into the relationships among human values, attitudes, norms, and behavior (Decker et al., 2012). This has resulted in significant advancements in our understanding of the thoughts and actions of people toward wildlife. More recently, HDW research began applying ecological theories and models to understand how humans function in and influence wildlife systems (Brøseth & Pedersen, 2000; Lyon & Burcham, 1998; Millspaugh, Brundige, Gitzen, & Raedeke, 2000; Proffitt, Grigg, Hamlin, & Garrott, 2009; Stedman et al., 2004). With better monitoring of spatially and temporally explicit human activity through comprehensive social-science surveys and increased public engagement in wildlife research (e.g., citizen science, community-based monitoring), there are new opportunities to explore human behaviors using research techniques generally applied to wildlife populations.

For example, with a spatially overlapping and temporally explicit dataset of human resource use and wildlife data, we can evaluate human interactions with wildlife that may advance our understanding of how they compete for resources. This requires thoughtful integration of social and biological datasets. This thesis integrates spatially explicit datasets of moose (*Alces alces*) hunters and of wolves (*Canis lupus*) to ultimately evaluate how two predators pursue a common resource, moose. Understanding competition is important for managers, and is especially pertinent within our study system, as moose exist at extremely low densities, but are a primary subsistence resource for humans and an obligatory prey item for wolves. We define subsistence as non-commercial “customary and traditional use” of wildlife and fish as legally defined by the State of Alaska (Fall & Wolfe, 2012).

Subsistence systems are an excellent example of social-ecological systems. Where HDW broadly examines the interaction of humans and wildlife, the theory of social-ecological systems (SES) is related to HDW in that it acknowledges humans are linked to the natural environment through complex interactions (Berkes, Colding, & Folke, 2003; Chapin et al., 2006). These interactions apply to any system where humans are actively using the environment to collect resources (Chapin et al., 2006; Folke et al., 2010; Kofinas et al., 2010). SES are complex and adaptive and operate within certain spatial bounds. Researchers have applied the SES framework to subsistence systems (Berkes et al., 2003) by identifying the key biological and human components and exploring their linkages. We applied the SES framework to infer where humans and wolves are directly or indirectly competing for moose.

An important linkage in our SES is competition between humans and predators. Humans have long acknowledged competition for game with predators. In an attempt to reduce competition and increase ungulate yield in regions of Alaska, some game managers have implemented predator “intensive management” programs to remove predators from a system (Boertje, Valkenburg, & McNay, 1996; Boertje, Keech, & Paragi, 2010).

We conducted our research on human hunters and wolves in the Yukon Flats, Alaska. The predator-prey relations in the Yukon Flats are unique because wolves and subsistence users pursue moose that are held at a low-density equilibrium primarily from predation. Our results present novel contributions to the literature by quantifying rural hunter access to moose, and characterizing wolf movement in a low prey-density system. Our results of human access to moose could supplement moose harvest estimates in the region, which are considered

unreliable (Andersen & Alexander, 1992), and our results of wolf movements provide the first such detailed information as to how wolf behavior may be unique in a low prey-density system. There is value to better understanding competition between humans and wolves, especially in a low-density system where each rely on moose. Our spatial datasets of human access and wolf locations have significant overlap, and we conclude by determining where the potential competition for a scarce resource, moose, was highest between wolves and humans.

HDW and SES researchers utilize interviews, surveys, or observations to gain insight into human perception, values, or utilization of their environment (Brinkman, Kofinas, Chapin III, & Person, 2007; Fulton, Manfredo, & Lipscomb, 1996; Manfredo, Teel, & Bright, 2003). Chapter 1 of this thesis focused on HDW by quantifying rural hunter access in the Yukon Flats, Alaska, through spatially-linked interviews. We chose this research topic because previous studies have only qualitatively surmised use area for subsistence resources (Caulfield, 1984; Stevens & Maracle, 2012), but a quantitative approach can yield firmer management information. This novel approach provided pertinent insight into resource use for our system and created a method that may be applied to other systems. Using results generated from subsistence hunter interviews, we applied a model of access to moose hunting areas. Harvest reporting is low among the subsistence communities in our study, and from our results we generated an estimate of harvest based on game densities similar to the best data available on reported harvest. As such, our method may provide an alternative to, or supplement, harvest-ticket reporting.

Wolves are a highly studied organism because of their charisma (Sergio, Newton, Marchesi, & Pedrini, 2006), pack social structures (Schmidt & Mech, 1997), status as a keystone predator (Ripple, Larsen, Renkin, & Smith, 2001; Wilmers, Crabtree, Smith, Murphy, & Getz, 2003), and relation to prey (Hebblewhite & Pletscher, 2002; Vucetich, Peterson, & Schaefer, 2002). The movements of wolves have been studied and documented in many high prey-density systems (DeCesare, 2012; Hayes, Baer, Wotschikowsky, & Harestad, 2000; McPhee, Webb, & Merrill, 2012), but almost no information exists on their movements when prey is just dense ($<0.20 / \text{km}^2$) enough for wolves to survive (Messier, 1985). In Chapter 2, we characterized movement paths (i.e., hunt paths) between moose kills by six packs in the Yukon Flats.

Competition between humans and wolves for a scarce and important resource, moose, is an example of a SES link. We conclude by applying what we learned about human and wolf space use to infer competition for moose.

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Chapter 1 Quantifying Rural Hunter Access in Alaska¹

1.1 Abstract

Despite hunter access influencing harvest success, few studies have quantified characteristics of hunter access. Based on spatially explicit interview data, we used GIS analyses to calculate access pathways and distances that rural hunters traveled to harvest moose (*Alces alces*) in Interior Alaska. We determined hunters were primarily utilizing river corridors. For 247 harvest locations, on average hunters traveled less than 1 km from the river corridor, and over half the harvests occurred within 25 km of the hunter's village. We used moose density estimates in the area being accessed by hunters to calculate annual moose harvest. Our results were similar to estimates from independent sources that used more standardized methods (e.g., agency household surveys). This suggests that our access-based approach has potential to provide an alternative method for estimating harvest intensity in areas where harvest report data are considered unreliable. Also, our findings demonstrated how insight on hunter access might help prioritize areas for active management.

1.2 Introduction

Along with game population size and seasonal distribution, a hunter's ability to access land controls the overall availability of the resource for harvest (Brinkman, Kofinas, Hansen, Chapin, & Rupp, 2013; Gratson & Whitman, 2000a; Millspaugh, Brundige, Gitzen, & Raedeke, 2000). An increase in the amount of spatial and temporal data on hunter interactions with

¹ Johnson, I., Brinkman, T., Britton, K., Kelly, J., Hundertmark, K., Lake, B., Verbyla, D. (2015). Quantifying Rural Hunter Access in Alaska. Prepared for submission to the Journal of Human Dimensions of Wildlife.

wildlife and wildlife habitat has increased our understanding of, and our ability to quantify how hunters use the landscape. Overall these data have demonstrated that hunters predominantly use easily accessible areas (Gratson & Whitman, 2000b). For example, white-tailed deer (*Odocoileus virginianus*) hunters concentrated effort within 0.8 km of a road 98% of the time in Minnesota, disproportionally killing deer in those areas (Fuller, 1990). Increased hunter access decreased moose (*Alces alces*) density in Ontario and increased the probability of mortality of elk (*Cervus canadensis*) in Idaho, whereas closing roads significantly decreased the number of elk hunters in a given area (Gratson & Whitman, 2000a; Rempel, Elkie, Rodgers, & Gluck, 1997; Unsworth, Kuck, Scott, & Garton, 1993). The development of access may quickly change the amount of hunting pressure in a region. In African communities, new logging roads facilitated access and increased legal and illegal harvest of game for personal use and commercial markets (Bowen-Jones, Brown, & Robinson, 2003). Given the strong link between hunter pressure, harvest, and access, game managers can benefit from estimating, monitoring, and incorporating the extent of hunter access into management plans.

Qualitative evidence suggests that access to subsistence resources in the Arctic may be as important to harvest success as abundance of subsistence resources (Brinkman et al., 2014; Chapin et al., 2010; Kofinas et al., 2010). However, few data are available to quantitatively assess this statement. We define subsistence as non-commercial “customary and traditional use” of wildlife and fish as legally defined by the State of Alaska (Fall & Wolfe, 2012). To date, few published studies have quantified characteristics related to rural hunter access to subsistence resources. Brinkman et al. (2014) examined the effect of fuel costs on access to subsistence resources and found that rising fuel costs have reduced subsistence activity (e.g.,

travel distance) by 60% in the last 10 years. Spatially explicit data on how and where game populations are accessed may aid game managers by providing insights into relative pressure on habitat and the resource. Spatially explicit data may demonstrate the importance of certain corridors and habitat types that facilitate or hinder hunter access.

Our research quantified access of subsistence hunters from several communities in Interior Alaska. Specifically, we quantified access to moose by five communities in the Yukon Flats using decades of spatially explicit documentation (e.g., traditional ecological knowledge (TEK)) of hunting patterns of subsistence users. TEK provides a tool for researchers to gain insight from area residents who are most familiar with the land and is defined as the insight gained from an individual or community based on their long-time, in-depth, and broad interaction with a species or use of an area (Huntington, 2000). TEK research has been shown to be an effective component of sustainable management and monitoring of local wild resources (Huntington, 2000; Polfus, Heinemeyer, & Hebblewhite, 2013). Moose are an ideal resource to quantify access in the Yukon Flats because they are a primary subsistence resource pursued by most hunters on an annual basis. Secondly, predominant access for moose occurs in September by using boats, which allows us to infer an access path with confidence (Van Lanen, Stevens, Brown, & Koster, 2012).

Game management goals usually include population level and harvest targets (Crichton 1993). Within Alaska, hunters are required to report information from their hunts (e.g., harvest success, location), and those compiled reports inform game managers if harvest targets were met. This information also helps when setting future management goals. Andersen and

Alexander (1992) demonstrated that harvest reporting via harvest tickets is low in rural communities because harvest tickets and a one-moose limit were not in line with traditional group hunting and sharing practices (McCorquodale, 1997). Traditionally in indigenous communities, a single hunter may harvest several moose in a season and share the harvest with several households. Andersen and Alexander (1992), citing a personal communication, suggested that only 40-50% of moose harvest was being reported in some rural communities. Schmidt & Chapin (2014) reported that levels of under-reporting were correlated with the percentage of community that was indigenous, the amount of moose-meat sharing among households within community, and the absence of an agency wildlife biologist in and road access to the community. In rural areas with under-reporting, wildlife managers are unable to effectively use harvest data to guide management (Klein, Moorehead, Kruse & Braund, 1999).

We propose an alternative approach to estimating moose harvest that may circumvent the under-reporting problems. Our research used spatially-explicit information on moose hunter access, estimates of moose density, and the best available data on moose harvest rates to answer the following questions: where are local communities concentrating their moose hunting activity, how many moose are available for harvest in areas accessible to moose hunters, and how many moose are harvested by communities on an annual basis from these areas. We addressed these research questions in remote areas of Interior Alaska where few communities are connected to the road network and high levels of under-reporting of moose harvest are thought to occur. Because communities are disconnected from the road network, travel may be limited by fuel cost (Brinkman et al., 2014), and qualitative data suggests that subsistence activity focused on navigable rivers in Interior Alaska (Caulfield, 1984), we

hypothesized that our quantitative investigation would reveal that moose hunter access concentrated around communities and near primary rivers. We quantified access based on TEK interviews and estimated harvest using game densities and access likelihood. This approach represents a novel way to inform wildlife managers of spatially explicit levels of harvest. More broadly, our research proposes that quantifying access to wildlife resources within a spatially explicit framework may provide insight on how to monitor and manage hunter access to achieve harvest goals in the Arctic and elsewhere. Also, our approach may provide a model for other systems where hunting pressure and success are strongly correlated to access.

1.3 Study Area

The Yukon Flats is located in eastern Interior Alaska and is bounded by the Brooks Range to the north and the White Mountains to the south (Figure 1-1). The Yukon River bisects the region, and at its center is the confluence of the Yukon, Porcupine, and Chandalar rivers. The Yukon Flats National Wildlife Refuge (Yukon Flats NWR) covers approximately 34,000 km² (8.6 million acres) and a majority of the Yukon Flats. It stretches approximately 350 km (220 miles) from east to west and 190 km (120 miles) north to south. Land ownership of the Yukon Flats is a complicated checkerboard pattern of private, state, and federal lands. Subsistence moose harvest is regulated under a “dual management system.” Harvest of moose on state lands (private lands included) is regulated by the Alaska Department of Fish and Game (ADF&G), and moose harvest on federal lands is regulated by the federal government under a Memorandum of Understanding (Fall & Wolfe 2012). Most of the Yukon Flats is within GMU subunit 25D; however, the Yukon Flats does bisect 25B to the east and 25A to the west (Figure 1-1). Within the GMU subunits, moose hunting occurs between August 25th and February 28th. Hunters are

allowed to harvest one bull moose per regulatory season. However, 89% of moose hunting often occurs in September before freeze-up and is predominantly conducted by boat (Van Lanen et al., 2012). In general, qualitative data suggests that moose are killed near rivers (Caulfield, 1984; Van Lanen et al., 2012). Moose populations within the Yukon Flats are at some of the lowest densities in the world (Gasaway et al., 1992; Lake, Bertram, Guldager, Caikoski, & Stephenson, 2013). Aerial estimates during November 2010 indicated 0.08 moose/km² in the western Yukon Flats (Lake, 2013). Based on the 2001 National Land Cover Dataset, the Yukon Flats is 67% boreal forest and 33% riparian areas. Boreal forests and riparian species include white spruce and black spruce (*Picea glauca*, *P. mariana*), white birch (*Betula papyifera*), aspen and poplar (*Populus tremuloides*, *P. balsamifera*), alder (*Alnus* spp.), and willow (*Salix* spp.) (Caulfield, 1984; Homer et al., 2007).

We analyzed moose hunting patterns for five communities within the Yukon Flats: Beaver, Birch Creek, Circle, Fort Yukon, and Arctic Village. The community of Arctic Village lies just beyond the northern border of the Yukon Flats NWR in the foothills of the Brooks Range, and Circle lies just south of the Yukon Flats NWR border. With the exception of Circle, these communities are disconnected from the road network. Some communities off the road network are accessible by barge during the summer and snow machine during winter, and all communities are accessible by plane year-round. Fort Yukon has the largest population ($N = 583$ (U.S. Census Bureau, 2010)) of all the communities in the Yukon Flats and is a regional hub. Populations in the other communities range from 33 to 104 people (U.S. Census Bureau, 2010). Residents of the communities are mostly Athabascan Indian (U.S. Census Bureau, 2010). Previous studies of subsistence in the Yukon Flats have outlined areas used for subsistence

(Caulfield, 1984; Sumida, 1988, 1989; Sumida & Andersen, 1990), but these studies have not quantified access within those areas.

Communities within the Yukon Flats have a mixed cash-subsistence economy. Wage employment is low, and subsistence harvest provides a significant source of nutrition for community residents (Wolfe & Walker, 1987). Subsistence resources also are critical to the cultural wellbeing of the region (e.g., potlatches) (Brinkman et al., 2014; Kofinas et al., 2010; Van Lanen et al., 2012). Primary subsistence resources include moose, caribou (*Rangifer tarandus*), fish (e.g., *Oncorhynchus tshawytscha*, *O. keta*, *O. kisutch*), berries, and firewood (Van Lanen et al., 2012).

Communities within the Yukon Flats have similar harvest patterns (e.g., timing, methods) (Caulfield, 1984). During 2009-2010, 77.7% of households in the Yukon Flats reported using moose, and 25.8% of households harvested a moose (Van Lanen et al., 2012). Sharing hunting equipment and harvest is common (Holen, Hazell, & Koster, 2012). Families who move to a different community often continue to use the same fishing and hunting areas (e.g., traditional use areas) they used in their previous community (Kofinas et al., 2010). Therefore, multi-generational subsistence areas are maintained despite family relocations. Reporting of harvest to management agencies is considered low in the study communities (Andersen & Alexander, 1992; Schmidt & Chapin, 2014). Therefore, game managers view harvest numbers as unreliable and seek an alternative method of determining harvested moose.

1.4 Methods

1.4.1 Hunter Interview Process

We used moose hunting data generated from a traditional land-use mapping project conducted by the Council of Athabaskan Tribal Governments (CATG). CATG's objective was to develop a "rigorous and legally defensible database" by systematically interviewing subsistence users in communities of the Yukon Flats to document knowledge of areas important for traditional and cultural activities such as subsistence (Thomas, 2005). Each community's Tribal Council drafted a comprehensive list of interviewees including hunters, elders, berry pickers, traditional medicine practitioners, tribal historians, and those (if any) currently living away from the community who had traditional knowledge of local harvest activities. CATG conducted structured interviews in 2005 and 2007 using a one-on-one format following a predetermined set of questions. During the interview, the interviewer would ask the interviewee to identify the local resources they had harvested (e.g., moose, ducks, berries, house logs). The interviewee was then encouraged to spatially document where and when the resource was used. If the interviewee was unable to clarify an exact location, the location was not mapped. Harvest locations were mapped on a transparent mylar sheet overlaid on a topographic map. Metadata were recorded for each use location in a separate data table. During the interview, interviewers collected use points (e.g., harvest location), use lines (e.g., trap line, access corridor) or use polygons (e.g., waterfowl hunting areas) depending on the feature type that fit the activity best. CATG also collected metadata on access method, years of use, and the cultural name of the harvest location. We digitized the data from CATG interviews in ArcGIS to a File Geodatabase and projected the spatial data in NAD Zone 6N.

For the purpose of this study, we explored moose harvest data because moose are a critical subsistence resource harvested on an annual basis, hunting corridors (i.e., rivers) could be inferred, and there was a statistically sufficient sample size ($n = 247$). Within the database, moose points were both described as “moose hunting” and “moose harvest” (hereafter, jointly referred to as harvest points). Interview participants reported moose harvest points over their lifetime and included data from 1941 – 2005. Some harvest points represented moose hunting areas used over consecutive years (e.g., 1960 – present). In these instances, we gave no extra weight to these points in our analysis because we did not consider multiple stacked points from one interview participant to be independent.

1.4.2 Spatial Analysis of Interview Data

We evaluated hunter access by identifying the river route and distance hunters traveled from (1) their respective communities to their moose hunting/harvest area, and (2) the distance they traveled from rivers. For this analysis, we pooled harvest points for all years due to strong spatial overlap in reported harvest locations across all the data. We calculated the Euclidean distance of the harvest points from the nearest navigable river at 1:1,000,000 scale, and the Euclidean distances of each harvest point to the hunter’s community of residence. We calculated the actual river distance to the point and ran a linear regression of the Euclidean distance and the actual river distance traveled to the harvest point. The regression showed a strong relationship ($p < 0.001$, $F = 454.6$, $df = 216$, $r^2 = 0.68$). This relationship was important because it demonstrated that using Euclidean distance in our final model of human access (methods below) translated into real distance traveled, making our model applicable to users. To distinguish levels of access, we binned Euclidean distances from rivers and each of the five

communities into five groups using Jenks Natural Breaks (JNB) (Figure 2). The JNB method is used in ArcGIS as a method for grouping data. In the method, the user selects the attribute to be classified and specifies the number of classes. A set of $k-1$ random or uniform values are generated in the range and utilized as initial class boundaries. The mean values for each initial class are computed, and the sum of squared deviations of class members from the mean values is computed. The values for each class are systematically assigned to adjacent classes with the goal of reducing the total sum of squared deviations. The procedure ends when within-class variance is as small as possible and between-class variance is as large as possible (De Smith, Goodchild, & Longley, 2007). We chose the JNB method to help draw out moose hunting patterns due to irregular groupings in the distances traveled in each community; because our analysis relies on visual interpretations of the data, it is important that the trends of each community be emphasized. Alternative methods such as equal interval or quartiles may have hidden visual data trends.

To translate the JNB distances into GIS layers representing spatially explicit routes and distances traveled, we created a multi-ring buffer around river access routes to harvest points. We calculated the access routes in ArcGIS 10.2 Network Analysis and buffered them based on the JNB binned values to create a layer of access distance from rivers. We calculated multi-ring buffers around each community based on the community's unique JNB binned values to create a layer of access distance from communities. Within each buffer ring of the access routes and communities, we calculated the "access index" representing the number of harvest points contained in the buffer divided by the total harvest points up to that buffer ring edge (i.e., first buffer ring equals 100% and is maximum attainable value). In other words, the access index

represents the percentage of moose hunters accessing up to the edge of the buffer distance; a higher index represents an area accessed by a relatively higher percentage of moose hunters.

Our goal was to create an access index that combined the reported distance from community and river. To accomplish this, we rasterized the access distance from rivers layer and access distance from each community layer (cell size = 100m), and we used ArcGIS raster math to add the six layers (i.e., 5 buffered communities and the buffered rivers) together into a final probability raster. We reclassified the final probability raster surface using JNB and three classes of high (1.38 – 2.52), medium (0.79 – 1.38), or low (0.12 – 0.79) access indices.

To extend the model of access to the entire study area (i.e., beyond rivers with reported harvest points), we used our access distance from community and river layers to identify other rivers and areas within our study area likely being accessed by moose hunters who did not participate in CATG's traditional land-use mapping project. These areas did not have reported harvest locations but were likely accessed by moose hunters based on distance to a community and navigability of a river by boat. We determined navigable river size by averaging the Strahler stream order value (SSO) (Strahler, 1954) along known travel routes. The average SSO was 4.33 ± 1.47 SD. Based on that, we selected all streams within travel distances reported by communities that did not have reported harvest points along them and had an SSO attribute value greater than 4. We buffered each of those rivers using the JNB values calculated from the travel routes. By extrapolating our model to rivers with characteristics similar to those of known travel routes, it encompassed rivers that did not have reported harvest locations. This was necessary as our sample sizes varied by community in both the number of interviews and the

number of points reported by the interviews (Table 1-1). Sample sizes in the smallest communities may adequately represent the variability in behavior of moose hunters from that community. However, in Fort Yukon, the population of which exceeds 500, the small sample size likely underrepresents the number of rivers used by hunters to access moose hunting areas. Extending our model to the entire area also enhances the model's relevance to game managers of moose who are evaluating population dynamics at a GMU scale.

We demonstrated wildlife management applications of the final model in three ways. First, to demonstrate the area of hunter access relative to the areas of GMU 25, we calculated the total area of access (e.g., maximum distance buffer around rivers and from community) as the number of cells multiplied by cell size of 0.1 km^2 . We divided this area by the entire GMU to estimate the percentage of the GMU being accessed by hunters. Second, to demonstrate the number of bull moose available (legally harvestable demographic) in areas being accessed, we calculated the total area of each probability class by multiplying 0.1 km^2 times the number of cells in each access index class (i.e., high, medium, low). We then multiplied the result by 0.016 bull moose/ km^2 (Lake, 2010). Important to interpretation of the number of accessible bull moose was that the density estimate (0.016 bull moose/ km^2) was based on post-peak hunt (e.g., September) surveys. This and several other factors (e.g., non-uniform distribution) contributed to a conservative estimate of numbers of accessible moose, as moose surveys also do not take into account the transient nature of rutting bulls that makes them more susceptible to hunters (Jason Caikoski, ADFG, pers. comm.) because moose are easier to see and moose counts on the Yukon Flats tend to be greater closer to rivers (Lake, 2010). While moose density post-peak hunt is not ideal, aerial surveys were not conducted prior to hunting season because

they are not socially acceptable, as data collection activities are perceived to disturb moose and impact hunter success.

1.5 Results

Based on 43 interviews in five communities, we identified 247 moose harvest points along or near rivers between years 1941 and 2005 (Table 1-1). On average, hunters traveled 0.9 km (SE = 0.6 km) from river corridors. Using JNB, 53%, 21%, 5%, and 21% of harvest locations occurred along navigable rivers between 0-24 km, 25-52 km, 53-86 km, and >86 km from the hunter's respective community. The average Euclidean distance from communities was 47 km (SE = 32 km).

The composite surface resulted in an access index (Figure 1-3) that ranged from 0.12 – 2.52. Areas with the highest composite access index value were accessed by the highest proportion of moose hunters. When we extrapolated distance findings to rivers around communities without reported harvest locations, we identified an access index of 0.13 – 2.43, similar to the areas with harvest points.

We applied the models of combined access index around rivers with and without reported harvest to create a final access index (Figure 1-3) and to estimate the number of legally-harvestable moose available in each access index level (i.e., low, medium, high) based on regional moose density estimates. The reclassified combined access index surfaces (Figure 1-3) contained 3,751 km² (17% of total) classified as high combined access index, 5,645 km² (25% of total) classified as a medium access index, and 13,300 km² (59% of total) classified as a low access index. The total access area was 22,697 km² (16% of GMU25). By applying a general and

uniform assumption of density of 0.016 (95% CI \pm 0.007) bull moose/km² (i.e. legally harvestable) to the high probability area, we estimated conservatively that 60 (95% CI \pm 26) legal moose were highly accessible to hunters from five communities. In medium access index areas, 90 (95% CI \pm 39) legal moose were accessible and 212 (95% CI \pm 93) legal moose were accessible in the low index area. Within the total access area, we estimate 363 (95% CI \pm 159) legal moose were available for harvest. Accounting for all households that report using moose ($N = 270$) within our study communities, we approximate that 0.22 (95% CI \pm 0.09), 0.33 (95% CI \pm 0.14), and 0.79 (95% CI \pm 0.34) moose were available per household in the high, medium, and low access index areas, respectively. In the total access area, we estimate conservatively that 1.34 (95% CI \pm 0.59) moose were available per household.

1.6 Discussion

This study quantified moose hunter access in rural Alaska. Similar to qualitative descriptions (Sumida, 1989; Sumida & Andersen, 1990; Van Lanen et al., 2012), we determined that hunters were using rivers. The traditional ecological knowledge dataset used in this analysis demonstrates the richness of data that can be collected through an interview process. For example, these data provided fine-resolution information that has not been captured well under the traditional harvest reporting systems that collect data at the broader scale of GMU sub-units or watersheds. The fine resolution of these TEK data provided practical insight into critical hunting areas. The accessed river corridors represent a small percentage (16%) of the total area (i.e., GMU) managed for a specific moose population goal and harvest number. During times with budget shortfalls, game managers may consider managing for and improving areas most accessed by users. Focusing management on this 16% of land may improve moose

harvest opportunities and alleviate conflict with non-local hunters by directing them to areas less utilized by local communities. Alternatively, if the goal was to maintain moose numbers, rather than a harvest amount, liberalizing harvest in areas with less access and restricting harvest in high access areas may be feasible.

Conflict between rural communities and non-local hunters continues to be an important issue in rural Alaska (Kofinas et al., 2010). Within the total access area, 40% of land was owned by Native corporations and 44% was managed by the U.S. Fish and Wildlife Service (USFWS). The remaining 16% of land was managed by the State of Alaska, Bureau of Land Management, National Park Service, and Department of Defense. These different entities may implement measures that increase apparent local moose densities in the access corridors through moose habitat improvement or through manipulation of habitat to increase moose sightability. Secondly, they may increase hunter access area through establishment of terrestrial trails (e.g., ATV) away from navigable rivers, which may be difficult to access ordinarily because of impenetrable characteristics (e.g., shrub vegetation) of the upland landscape. Currently, the few established ATV trails around communities are used by moose hunters, but only offer day-hunt opportunities (Van Lanen et al., 2012). All of these management strategies have direct benefit to subsistence users and may also benefit the non-local hunting experience.

We linked our access model to estimates of bull moose density (0.016 moose/km^2 ; Lake 2010) to estimate the number of harvestable moose (363 moose) in the area accessed by hunters on an annual basis. If we multiply this estimate by the mean harvest success rate across Yukon Flats communities (27-46%; (Community Subsistence Information System, 2015; Van

Lanen et al., 2012)), we calculate between 98 to 167 moose may be harvested annually. Using door-to-door household surveys, Van Lanen et al. (2012) estimated that Fort Yukon, Beaver, Birch Creek, and Circle harvested 88 moose in 2010. Although the Van Lanen et al. (2012) estimate is 24% of our modeled estimate of 363 available moose, their study does not account for moose harvest in other communities (Arctic Village, Venetie, Chalkyitsik, Stevens Village) along the access pathways within our final model (Figure 3). Estimated annual moose harvest in those communities was roughly 26 moose (Stevens & Maracle, 2012) bringing the total community harvest of moose to around 114 moose. This estimate may be conservative considering the potential for underreporting in rural communities in Alaska (Andersen & Alexander, 1992; Schmidt & Chapin, 2014). Thus, our estimates derived from an evaluation of access (98-167) are firmly within the plausible range of estimates from independent sources using other methods.

The similarities in estimates suggests that fine-scale information on access characteristics may provide an alternative method to estimating harvest and may be a more acceptable approach in communities that are reluctant to report harvest through agency channels (Andersen & Alexander, 1992; Schmidt & Chapin, 2014). Rather than rely solely on reported harvest of moose or GMU-wide bull moose densities to inform decision making, evaluation of moose densities in accessible areas and how that changes over time could provide useful criteria for management. This would require development of smaller-scale population survey areas termed “analysis areas” by Kellie and DeLong (2006), in combination with the larger areas that were already surveyed (Lake et al., 2013).

Our results indicated that hunters from Fort Yukon travel farther than any of the other communities (Table 1). Fort Yukon hunters may be traveling to traditional use areas or moving to areas with less hunting pressure and bypassing areas where moose could be found (Van Lanen et al., 2012). We define traditional use as factual knowledge of both past and present uses of the land and may include social and historical factors that influence the traditional land use of a population of people (Usher, 2000). Because Fort Yukon is a regional hub with a larger population that includes residents with family in neighboring communities, it was a reasonable assumption that some traditional use areas were outside of Fort Yukon and closer to other communities. The best example of this was the high access of moose hunting in the Chalkyitsik region and Draanjik River (Black River). These data originate from Fort Yukon interviewees and demonstrate high access to an area up to 165 km (Euclidean distance) from Fort Yukon. Our results are in line with qualitative work by Caulfield (1984), which found Fort Yukon moose hunters used hunting areas in Beaver, Chalkyitsik, Birch Creek, and Circle.

Our study represents an innovative way to model and quantify access for subsistence users in an arctic or sub-arctic system. This hunting system is dynamic and may be strongly affected by changing climate, river conditions, and social and economic factors in the future. For instance, the ability to access resources by boat or snow machine may be directly impacted by rising fuel costs (Brinkman et al., 2014) or changes in hydrology (Kofinas et al., 2010). Responding to fuel prices and risk to subsistence equipment from low river flow, hunters already report taking fewer, but longer hunting trips (Brinkman et al., 2014, Kofinas et al., 2010). This may reduce hunter effort (e.g., time and distance traveled) and success during each moose-hunting season. Based on this, future studies may examine changes in access distance

and effort over time with changing socio-economic costs and could include how unique hunter demographics or user groups may access hunting areas differently. Of particular interest, hunter demographics and access could differ between private and public-land hunting and provide managers with estimates of harvest on private lands. Researchers may refine results by including a dynamic of hunter preference using popular resource selection functions (Boyce & McDonald, 1999; Manly, McDonald, Thomas, McDonald, & Erickson, 2002).

River access within our study area were analogous to road or trail access within many hunting systems and enables our model to be applied to hunting systems where hunter access is driven by landscape characteristics or regulations. Along with access characteristics, game managers may consider changes in hunter demographics to forecast hunter pressure or harvested game based on a growing or declining population. Within North America, ungulate hunting success is strongly associated with road density (Fuller, 1990; Hayes, Leptich, & Zager, 2002; Rempel et al., 1997) and road closures on federal lands are a method of decreasing harvest. Spatial modeling of hunter access from roads may inform game managers of the total area impacted by road closures, and with known ungulate densities, allow them to estimate the number of animals impacted by the closure. If the goal of management was not to create greater harvest opportunities, but instead maintain population levels, modeling future access may give managers a tool to proactively restrict quotas in a region, instead of waiting for hunter harvest information to inform their decision-making. With a prior understanding of the game harvest as a response to hunter access, game managers could model the effect of newly established roads or trails on harvest. In Africa, applying access distance to newly established

logging roads could identify areas where game harvest is not occurring intensely, thus identifying conservation regions (Bowen-Jones et al., 2003).

1.7 References

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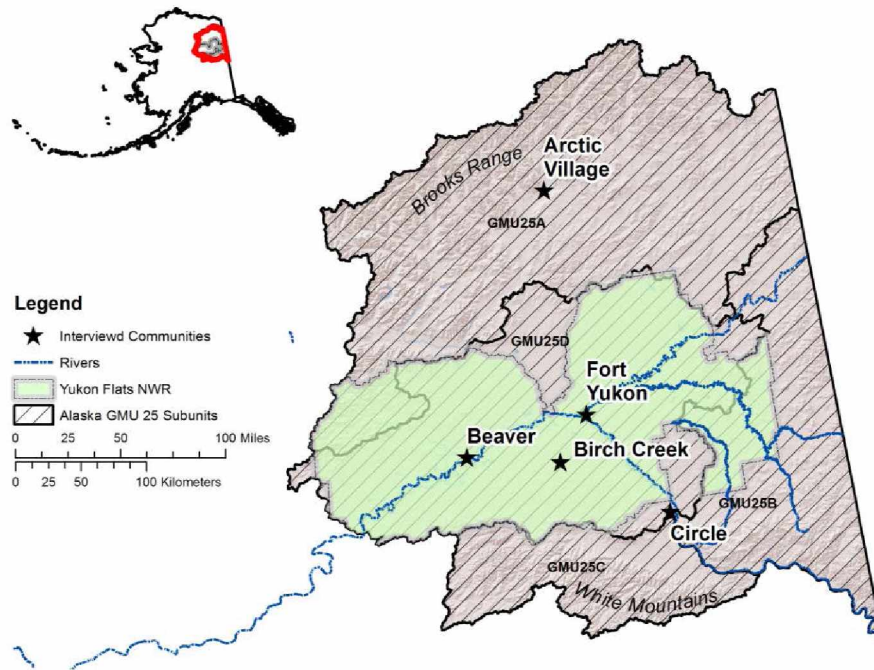


Figure 1-1: Study area including the boundary of the Yukon Flats National Wildlife Refuge and interviewed communities within the Yukon Flats included in the analysis of this paper.

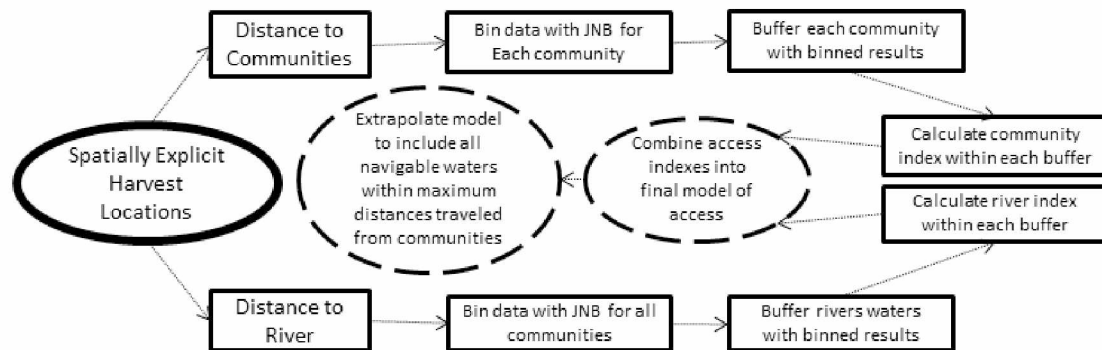


Figure 1-2: Conceptual model of data analysis. The input data are contained within the bold oval. GIS processes are within rectangles, and the final model is within dashed ovals.

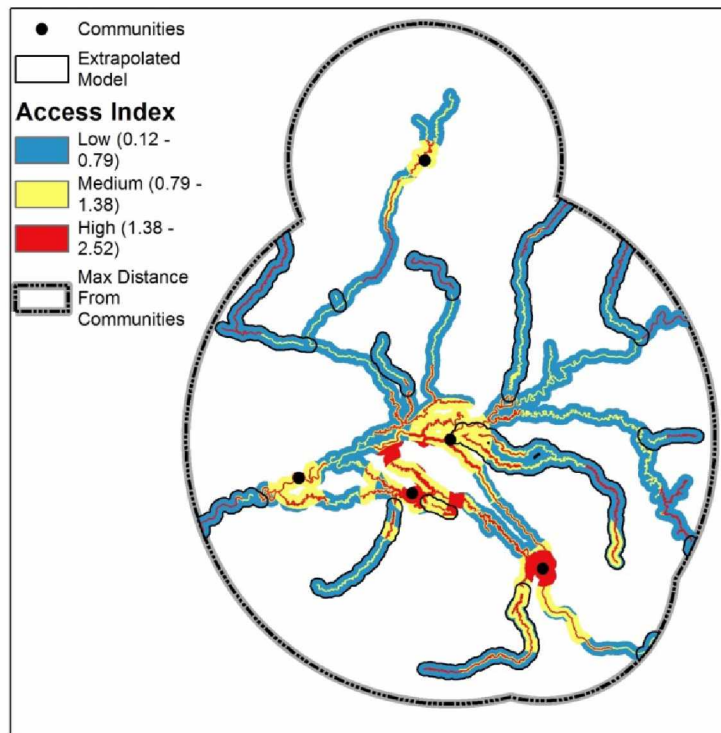


Figure 1-3: Combined access index surface. Rivers had a Strahler stream order value >4, and were within reported travel distances of communities, but that do not have reported harvest locations. Surface is based on raster math addition of access index values of distance from rivers and community. In the model, blue areas indicate lower probability of access, and red indicates a higher probability of access.

Table 1-1: Summary of JNB of the Euclidean distance of harvest points from community of residence. The number of points in parentheses is the number of moose harvest points falling inside of that break area.

Community	n (number interviews)	Break distance km (# pts)					Mean km \pm SE
Fort Yukon	11	25.9 (13)	47.6 (14)	86.0 (5)	134.8 (16)	165.0 (36)	100.3 \pm 53.4
Arctic Village	4	12.6 (5)	21.3 (3)	30.0 (3)	43.8 (3)	85.4 (1)	25.8 \pm 20.7
Beaver	9	4.1 (4)	14.2 (9)	19.7 (11)	29.2 (3)	41.2 (1)	15.5 \pm 8.2
Circle	8	11.4 (12)	26.7 (9)	52.6 (12)	62.6 (3)	82.7 (3)	32.4 \pm 24.0
Birch Creek	11	6.6 (16)	13.4 (28)	23.2 (22)	32.7 (6)	40.8 (8)	15.0 \pm 10.5
All	43	--	--	--	--	--	47.0 \pm 32.0

Chapter 2 : Hunting Behavior and Habitat Selection of Wolves in a Low-density Prey System During Winter

2.1 Abstract

To evaluate how a coursing predator maintains kill rates, we extend on a study that found that winter kill rates of wolves (*Canis lupus*) in a very low prey-density system were similar to kill rates in high prey-density systems. We used global positioning system collars to characterize wolf travel paths between kills to evaluate wolf travel speed, movement distance, and time between kills. Apart from the path characterization we calculated the handling time of each kill. We compared these results to literature in high prey-density systems and found that wolves in a low prey-density system are not traveling faster (0.6 km/hr), but instead farther (65 km) and with a longer time interval between kills. Using a generalized linear mixed effect model, we also evaluated resource selection by wolves and concluded that similar to wolves in high-density systems, wolves in our system were selecting for river corridors that enable efficient travel and likely bring them into contact with prey. These results are the first to characterize movements of wolves in a low prey-density system, and our finding of long travel distances help explain large wolf territories at low prey densities. This may aid management models by understanding the effect of changing ungulate densities on wolf movement patterns and densities.

2.2 Introduction

More than forty years ago, Mech (1970) expressed that little science had been conducted in regard to wolf (*Canis lupus*) hunting behavior and that conclusions were based on

“hearsay” and “interpretations of tracks in the snow” by non-objective observers. Since that time, radio-telemetry methods and most recently global positioning system (GPS) collars have yielded remarkable insights into kill paths (DeCesare, 2012; McPhee, Webb, & Merrill, 2012a), handling time (i.e., the amount of time it takes to subdue, kill, and consume prey) (Hayes, Baer, Wotschikowsky, & Harestad, 2000), and kill rates (Hayes et al., 2000; Lake, Bertram, Guldager, Caikoski, & Stephenson, 2013; Messier, 1994) of wolves when pursuing ungulate prey. Throughout their global range, a suite of spatially driven studies of wolf movement and behavior has been conducted, but these studies have occurred in regions with medium to high prey density (Eriksson, 2003; McPhee et al., 2012a; Zimmermann, Wabakken, Sand, Pedersen, & Liberg, 2007). No studies of wolf movements have been conducted in areas with relatively low prey densities of large-bodied prey (e.g., moose (*Alces alces*)).

The presumption that prey is scattered randomly across the landscape and that predators search randomly (Holling, 1959) has been disproven. Predators select for a variety of conditions relating to habitat, prey density, or prey vulnerability that may increase kill rates or efficiency (Hebblewhite, Merrill, & McDonald, 2005). Within boreal forests, wolves show selection for elevation and for edge habitat or open habitat where prey is vulnerable when pursuing ungulates (DeCesare, 2012; Kunkel & Pletscher, 2000; McPhee et al., 2012a; Mech, Smith, & MacNulty, 2015). Wolves are a coursing predator and hunt continuously while on the move (Mech & Boitani, 2010; Mech, 1970) and may optimize their travel paths to encounter the greatest amount of prey (McPhee et al., 2012a).

Low-density ungulate-predator systems likely function differently than high prey-density systems. Movements in low-density and large-bodied prey systems may be different from high-density and large-bodied prey systems because previous studies on predators have demonstrated selection for prey density, rather than prey habitat (Keim, DeWitt, & Lele, 2011; McPhee et al., 2012a). In a low prey-density system, we assume prey density is less likely to drive selection because prey are more likely to be spread out more thinly compared to high densities, but predators still need to kill enough prey to survive. To compensate for low-prey densities and maintain caloric requirements, predators may need to change behaviors or habitat selection that could include the rate of speed they travel, the amount of area searched or distance traveled, the habitat or terrain they use, or selection for prey density (DeCesare, 2012; McPhee et al., 2012a; Mech & Cluff, 2011; Moffatt, 2012; Vander Vennen, 2014).

To address the impact of wolf predation in a single-prey system of low prey densities, a study was initiated in 2008 to examine moose kill rates of wolves in the Yukon Flats, Alaska, where moose are the sole ungulate prey and occur at low densities (<0.20 moose/km²) (Alaska Department of Fish and Game, 2010; Lake, 2010; Lake et al., 2013). During the study, in 2009-2010, GPS collars were deployed on six wolf packs. Regular flights were flown to identify whether clusters of GPS locations were kill sites. Lake et al. (2013) demonstrated that kills per wolf-day were similar to reported kill rates in high moose-density systems and wolf mean protein intake was similar to high prey-density systems reported by Mech & Peterson (2003). Per-wolf rates may be maintained across densities through the adjustment of territory size (Kittle et al., 2015); however, it is plausible that wolves also may modify their movement behavior and characteristics such as habitat selection.

To explore the possible changes in movement behavior, we analyzed travel paths, rates of speed, distances traveled, and underlying habitat characteristics of wolves from six packs in the Yukon Flats and compared them to movements of wolves in systems of higher prey density. Our research objective was to describe the movement behavior and habitat selection of wolves on the move (e.g., excluded resting and kill site behavior) in a low-density prey system. Our study is the first to characterize wolf movements in a low prey-density system. We calculated descriptive statistics of wolf movement. Along with those statistics we hypothesized that wolves utilized landscape characteristics that aid in efficient travel. We predicted they would use non-forested areas or river corridors. Such use of river corridors may also result in greater numbers of prey encountered, as moose may preferentially forage in these areas in winter (Baigas, Olson, Nielson, Miller, & Lindzey, 2010; MacCracken, Van Ballenberghe, & Peek, 1997).

2.3 Study Area

Our study was conducted in the Yukon Flats of eastern Interior Alaska (Figure 2-1). The Yukon Flats is bounded by the Brooks Range to the north and the White Mountains to the south. Elevations within our study area range from 91m to 912m, but most of the area is low and flat. The Yukon River bisects the region and at its center is the confluence of the Yukon, Porcupine, and Chandalar rivers. The Yukon Flats National Wildlife Refuge (Yukon Flats NWR) covers approximately 34,000 km² (8.6 million acres) and a majority of our study area. It stretches approximately 350 km from east to west and 190 km from north to south. Based on the 2001 National Land Cover Dataset, the Yukon Flats is 67% boreal forest and 33% riparian areas. Boreal forests and riparian species include white spruce and black spruce (*Picea glauca*,

P. mariana), white birch (*Betula papyifera*), aspen and poplar (*Populus tremuloides*, *P. balsamifera*), alder (*Alnus* spp.), and willow (*Salix* spp.) (Homer et al., 2007).

The climate of the Yukon Flats is classified as sub-arctic and characterized by long cold winters (November – March) and short dry summers (May – August). Temperatures are seasonably variable, but can attain -51°C in January and 37°C in July. The dry climate generates snow depths much less than 90 cm, which is considered a threshold that results in changes in moose movement and survival (Coady, 1974; Gasaway, Stephenson, Davis, Shepherd, & Burris, 1983; Gasaway et al., 1992). During our study period, snow depths at 2 snow stations (Lower Beaver Creek and Vunzik Lake) measured 69 and 48cm, respectively. The 10-year average at those stations was 52cm and 64cm, respectively (Natural Resources Conservation Service, 2015)

Aerial estimates during November 2010 indicated 0.08 moose/km² in the western Yukon Flats (Lake, 2013). Wolf densities in the Yukon Flats are estimated at 3.4-3.6 /1,000 km² (Lake, Caikoski, & Bertram, 2015). Moose densities are thought to remain at a low-density equilibrium due to high calf mortality from bears (*Ursus americanus*, *U. arctos*) and adult mortality from wolves, combined with illegal harvest of cows (Bertram & Vivion, 2002; Gasaway et al., 1992). Within the Yukon Flats, moose are the primary food source for wolves, with occasional takes of snowshoe hare (*Lepus americanus*) or beaver (*Castor canadensis*) (Lake et al., 2013). Caribou (*Rangifer tarandus*) are not common in the area.

2.4 Methods

2.4.1 Wolf Capture

Wolves were chemically immobilized by darting from a helicopter (U.S. Fish and Wildlife Service Region 7 Animal Care Protocol no. 2008022), beginning in November 2009 in the region of Beaver, Alaska (Figure 2-1). Further details of wolf immobilization are described in Lake et al. (2013). Nine wolves from six packs were marked with Telonics model TGW-3580 GPS radio collars. The GPS collars recorded locations at three-hour intervals and had a life expectancy until May 2010. All data were accessed from the collar following recapture in April 2010.

Moose kill site locations were determined by Lake et al. (2013), using aerial surveys coupled with an analysis of location point clusters. Aerial surveys were flown weekly and during two approximate two-week periods in late winter, surveys were flown daily. Webb, Hebblewhite, and Merrill (2008) reported that a four-hour GPS interval was sufficient to identify 100% of kill sites by wolves on large-bodied prey, such as moose. Lake et al. (2013) used three-hour intervals and reported no errors related to incorrectly classifying a kill as a non-kill. Hence, they did not omit any kills. At the conclusion of their study, they identified thirteen point clusters of seven locations or more where flights did not confirm if a kill existed; if the point clusters were classified as a kill, but were instead a rest site, a commission error (i.e., classifying a rest cluster as a kill cluster) may occur. The six packs were monitored for different amounts of time. Four packs (Hodzana, Lost Creek, Beaver Creek, Crazy Slough) were monitored from November 11, 2009 – March 31, 2010. The Hodzana Mouth pack was monitored from November 11, 2009 through January 2010 when all individuals were killed by a competing pack. The Bald knob pack was monitored from December 2009 – March 31, 2010

(Table 2-2). All GPS collars demonstrated a high fix success (mean = 98%, range = 96 – 99%) rate, which was attributed to flat terrain and lack of canopy (Lake et al., 2013).

2.4.2 Dataset Preparation

We chose one wolf from each pack to represent all movements of the pack. We justify that decision based on synchronous movements of wolves in packs with two collared individuals (Metz, Vucetich, Smith, Stahler, & Peterson, 2011). Second, no pack maintained two operating collars for the entire winter due to mortalities, collar slippage, or collar failure. In the final dataset, we standardized the GPS data for each pack by removing points from capture up to their first kill and after the date of their last kill to collar retrieval. In the analysis, we included kills that were confirmed through aerial observation and location clusters that lasted longer than one day ($n = 10$ fixes) where the model of Lake et al. (2013) predicted the cluster was a kill. For each individual, we characterized the resulting GPS point data into four distinct behavioral classes that have been used in previous studies to characterize wolf travel (DeCesare, 2012; McPhee et al., 2012a), hereafter, referred to as “path characterization”. They included presence at kill site, resting, kill-site revisits, and traveling. We characterized kill site points as points around kills as determined through aerial surveys, clustering, and tracking conducted by Lake et al. (2013). We characterized rest points as consecutive points within travel paths that did not change more than 26m from the last point (i.e., in three hours). This distance was the approximate maximum accuracy of the GPS location (Adams, Dickinson, Robertson, & van Heezik, 2013), hence any points that did not move more than that could be considered the same location. Revisits included all points where a wolf returned to a kill and remained there 6 hours (i.e., two fixes) or more. Traveling included paths between kill sites, but excluded rest

points and all but the first revisit point at the kill. We maintained the first revisit point to keep the travel path intact.

2.4.3 Data Analysis

We derived several descriptive statistics from our path characteristics for comparison with other studies of wolf movement based on the published literature. These statistics included mean and standard deviation of handling time (days), mean and median days spent traveling (time between kills), mean and median distance (km) traveled, and mean and median travel speed (km/hr). Days spent traveling and travel speed were strongly skewed right and reporting their standard deviations would be inappropriate. We define handling time as the interval between when the kill began and when the wolf left the kill for more than 24 hours. We calculated the travel speed by dividing the segment length (i.e., distance between two GPS points) by the total time elapsed during that segment. For each pack we generated an activity budget. In the activity budget, we calculated the percentage of time spent traveling, at kill sites, revisiting kills, and resting based on our path characterization. To examine pack differences by pack size, we log transformed the handling time, time between kills, and travel distances, and used an analysis of covariance test (ANCOVA) to test for differences while controlling for pack size. If a difference was detected by the ANCOVA, we used a t-test with a Bonferroni adjustment to determine which packs differed. We compared these descriptive statistics with previously published literature on wolf travel speed, handling time, traveling distance, and days between kills within large-bodied prey systems. We chose these parameters because they are quantifiable, comparable to previous literature, and are behaviors that wolves can modify to adapt to a low prey-density system.

We examined underlying habitat selection during travel to aid with inference of our movement statistics output. We hypothesized that wolves were utilizing corridors such as rivers or habitats with minimal travel barriers to enable efficient travel (i.e., travel with the least amount of energy expended), and our covariates were chosen to test corridor usage. We defined a corridor as a landscape or habitat feature that enhances the movement of an animal (Bennett, 1999). Previous studies have associated wolves with linear corridors that may increase speed up to 2.8 times over forested habitats (James, 2000). In the winter, rivers become frozen and hard packed with snow, reducing energetic expenditure during travel. For instance, river corridors are used heavily enough by wolves that caribou may avoid rivers as an anti-predator strategy (Bergerud & Page, 1987). We assessed habitat selection while traveling using a resource selection function (RSF). RSFs are mathematical functions that tease apart use as a proportion to availability (Manly, McDonald, Thomas, McDonald, & Erickson, 2002). We used ArcGIS 10.2 (ESRI, 2014) to gather underlying landscape characteristics of wolf use points (GPS locations). All point data and underlying covariate layers were transformed to Universal Transverse Mercator (UTM) Zone 6. UTM zone 6 is appropriate for measuring distances between points in our study region. In order to maintain statistical power, we only chose biologically plausible covariates that we thought could be related to wolf travel paths (Table 2-1). These landscape characteristics were used as covariates in our RSF and included distance to rivers, distance to waterbodies, and distance to ridgelines. We measured distance to rivers and waterbodies as the distance from a point to the nearest river or waterbody of the high-resolution National Hydrography Dataset at a scale of 1:24,000 (Geological Survey (U.S.), 2015). We measured distance to ridges as the distance of points to ridges derived from a 17-m

resolution digital elevation model. We used the National Landcover Dataset (NLCD) from 2001 to generate underlying categorical habitat variables. We grouped NLCD into four broader categories based on habitat height. NLCD₁ was just the water NLCD class, which includes water bodies or rivers greater than 30x30 meters in width or area. NLCD₂ included shrub land cover of medium height. NLCD₃ included tall tree classes, and NLCD₄ included riparian or wetland classes with short or grassy vegetation. We believe these NLCD categories create efficient travel corridors in open habitats (NLCD₁, NLCD₄) and create barriers to travel in tall or medium vegetation-height habitats (NLCD₃, NLCD₄) (James, 2000).

We determined if there were differences between observed and expected use of categorical variables by building a contingency table of use and expected use for each of the NLCD groups (1, 2, 3, 4). We generated expected values by calculating the percentage habitat available within our available extent (i.e., the 95% kernel density estimate (KDE)) and multiplying the percentage by the sample size of travel locations ($n = 2,385$, Table 2-3). We conducted a Pearson's chi-square test in R (R Core Team, 2014).

We bolstered the results of the chi-square test by building an RSF model that controlled for variation within each pack. We used a generalized linear mixed-effects model (GLMM) with a logit link and a random intercept for each pack (DeCesare, 2012). Our model choice controls for autocorrelation of locations within a pack, and selection by an individual wolf would be expected to be more similar within the pack, than between packs (Hebblewhite & Merrill, 2008). Our RSF models compared underlying characteristics at used (1) and random available locations (0). Available points were generated within a 95% Kernel Density Estimate (KDE) area

(Houle, Fortin, Dussault, Courtois, & Ouellet, 2010) at a 1-use:1-available ratio. By utilizing 95% KDE, the analysis focused on the core home range of the wolf (DeCesare, 2012; Houle et al., 2010). We utilized a 1:1 ratio for each pack because the number of points for each pack in the dataset ranged significantly (Table 2-2), and a pooled sample size of 5,461 random points should adequately characterize the underlying data (DeCesare, 2012; Johnson, Nielsen, Merrill, McDonald, & Boyce, 2006). We built our RSF model in R using the lme4 package and glmer function (R Core Team, 2014). To help with model stability and convergence, we scaled continuous variables by subtracting the mean and dividing by the standard deviation. NLCD classes were input with “dummy indicator variables”, with NLCD₁ being the reference regressor. Model selection was based on the corrected Akaike Information Criterion (AIC_c) (Anderson, Burnham, & White, 1998; Gillies et al., 2006), with the model that best described the data having the lowest AIC_c model score (Table 2-3)

2.5 Results

Our analysis dataset contained 5,561 locations from six packs, and the number of locations from each pack ranged from 499 – 1,123 (Table 2-2). All kills were of moose. On average, wolves spent 40.5% of their time traveling, 43.7% at kill sites, 6.8% revisiting kill sites, and 6.8% resting (Table 2-6). The amount of time that wolves spent revisiting kill sites was highly variable among the packs. The Beaver Creek pack spent only 0.2% of its time revisiting old kills while the Lost Creek Pack spent 19.7% of its time revisiting old kills. Time spent traveling was similar among all packs (40.5%) except Hodzana Mouth, which spent only 26.5% of its time traveling. In turn, Hodzana Mouth spent 59.5% of its time at kill sites – the highest among all packs.

We analyzed 68 unique paths to kills during our study period. The number of kills varied by pack, and the largest packs made the most kills. The maximum handling time was 16 days and mean handling time was 4.0 days ($SD = 2.5$) for all packs (Table 2-2). While controlling for pack size, the log-transformed handling time of Beaver Creek was significantly different than Hodzana Mouth (ANCOVA $p = 0.027$, $df = 5$, $F = 2.73$, t-test $p = 0.039$). Average days between kills (ANCOVA, $p = 0.17$) and travel distance between kills (ANCOVA, $p = 0.39$) were not significantly different among packs. The maximum number of days between kills was 17.75, the median was 5.6, and the mean days between kills was 5.9. The maximum distance between kills was 263 km and mean travel distance was 65.2 km. Log-transformed travel distances and times between kills were highly correlated ($p < 0.001$, $r^2 = 0.85$, $df = 56$, $F = 340.9$). Median travel speed was 0.4 km/hr and mean travel speed was 0.6 km/hr. The results of Pearson's chi-square test showed a significant difference among use and expected use of habitat types (Pearson chi-square = 317.86, $p < 0.0001$) (Table 2-3). We used the results of the GLMM to provide statistical rigor to this test.

We selected our final RSF GLMM model by using the smallest AIC_c and would consider models within two points of the lowest AIC_c . Based on AIC_c our global model achieved the best model fit (Table 2-4) and converged successfully. In the global model, coefficients of $NLCD_2$, $NLCD_4$, the scaled distance to water, and the scaled distances to ridges were large compared to their standard errors, suggesting that the factors were significant to the model (Table 2-5). Coefficients of $NLCD_3$ were not significant. The coefficients of the analysis show very strong selection against $NLCD_2$ and mild selection against $NLCD_4$. A large, negative coefficient for distance to water suggests that as distances from water increase, the probability of selection

decreases. To a lesser extent, a smaller, negative coefficient suggests that as distance from ridges increased, selection decreased.

2.6 Discussion

The results of the aerial survey and location cluster analysis to identify all potential kills without omission error by Lake et al. (2013) gave us certainty in our results and that we had the necessary information to create a detailed path characterization for each wolf. We compared our results to other winter studies of wolf movement that analyzed GPS data and were in large-bodied prey systems (Table 2-7). Overall, in our low-density (<0.2 moose/km²), single-ungulate prey-system, wolves were traveling farther in search of prey than wolves in systems of higher prey-densities (Table 2-2). Our result of 65.2 km between kills was 2.4 times greater than the search distance reported by Moffatt (2012) of 27.4 km. In these high-density systems, and based on our findings, we speculate that wolves travel less distance because vulnerable prey is encountered at greater rates and because they were selecting for areas of high prey-density. Search time was significantly related to search distance, and we found a strongly significant relationship between amount of time between kills and distance traveled. This is expected for a coursing predator and demonstrates that wolves in our low prey-density system were ranging far distances over many days. Wolves, and coursing predators in general, rely on encountering vulnerable prey to make a kill (Mech et al., 2015). In our low prey-density system we expect the number of vulnerable prey encountered to be less than a high prey-density system. On long searches, wolves may be either not finding prey at all, or they may not be encountering vulnerable prey.

We compared our results of travel speed (0.6 km/hr) to previously published literature and found no evidence that wolves travel faster than in high prey-density systems. Average travel speed was similar to that reported by Vander Vennen (2014), who reported 0.2 – 0.7 km/hr. Travel speeds were slower than 1.2 km/hr in a high prey-density system reported by Gurarie, Suutarinen, Kojola, and Ovaskainen (2011). Maximum wolf travel speed (6.3 km/hr) in our system was less than wolves observed over the tundra (8.7 km/hr) (Mech, 1994). Lack of a difference in our low prey-density system suggests that wolves may be traveling as fast as they were efficiently able to in any prey-density. Alternatively, variation in reported speed is introduced based on the GPS interval used in the study and if the researcher reports speeds over the travel route or at a specific instance. Because wolves were traveling longer and not traveling faster, time between kills must be greater.

Average time to kill (5.9 days) was 1.4 times greater than Moffatt (2012)(3 days), whose system was characterized by moose as the primary prey. McPhee, Webb, and Merrill (2012b) reported that average time to event in their high-density system was 5.3 days, which is similar to time to event in our low-density system (5.9 days). Sand, Zimmermann, Wabakken, Andr n, and Pedersen (2005) report in a very prey-dense system of moose that time to kill was approximately 4 days. Long amounts of time to kills may require that wolves optimize kills by consuming everything possible, thus adding to long handling times.

Handling time was longer in our study system than previously reported studies with large-bodied prey (Eriksson, 2003; Hayes et al., 2000; Sand et al., 2005). We found a difference in handling time between Beaver Creek (8 wolves) and Hodzana Mouth (5 wolves) packs;

however, seeing as another pack (Hodzana) had 5 or more animals and was not significantly different than Beaver Creek, pack size was likely not explanatory. The difference in handling time may be due to pack heterogeneity, as Hayes et al. (2000) found no significant difference in handling times based on pack size and they found that handling time for adult or calf moose (2.9 and 2.6 days respectively) was not significantly different. Alternative to pack size, longer handling time may also be a function of prey density. Long handling times may indicate that wolves were food-limited and completely consumed the kill before initiating another hunt. Investigations on the ground at a sample of kills by Lake et al. (2013) found that kills were completely consumed before wolves revisited, which was in contrast to Eriksson (2003) who documented partially consumed moose in their very high prey-density system. Partial moose consumption in Scandinavia may be linked to high disturbance rates of wolves at kills by humans (Sand et al. 2005). In contrast, disturbance of wolves by humans in the Yukon Flats is low and is unlikely to change their behavior.

Wolves revisited kill sites frequently and that frequency may be unique to our system (Table 2-6). Percentage of time spent revisiting a kill may be a function of pack size, as the Beaver Creek pack, the largest pack with eight individuals, revisited kills the least amount of time (0.2%). In contrast, Lost Creek, Crazy Slough, and Bald Knob, with two, four, and four individuals respectively, revisited kill sites from 7.8 – 19.7% of their total time. Zimmermann et al. (2007) reported that 35% of moose kills were revisited. Pooling all packs, our results were consistent with their findings, as wolves in our study revisited 30% of kill sites. However, as an exception to this, our results demonstrate that the smallest pack, Lost Creek, revisited 70% of their kills. In our system where moose kills were consumed before the wolves start to hunt

again, we are not sure what benefit there is to revisiting kills. Perhaps revisits to kills were simply driven by individual heterogeneity in decisions by wolves, or kill revisits occur most frequently along common travel paths (Eriksson, 2003).

Our hypothesis that wolves are using areas that enable efficient travel during long travel distances was supported by the results of the RSF based on habitat types and selection for distance from rivers. Our results were consistent with other studies that report selection for linear corridors, including rivers or seismic lines (James & Stuart-Smith, 2000; McPhee et al., 2012a). By strongly selecting against barren, shrub-scrub, and dwarf scrub habitat classes, wolves were selecting against dense travel barriers. These habitats are characterized by willow, birch, and alder, which can be nearly impassable. Of our two continuous variables, distance to water was the most strongly selected for. Our results suggest that wolves were selecting for water bodies or riparian corridors to travel. Selection for efficient travel corridors likely explains wolf habitat use over long-distance movement. However, riparian corridors and areas without dense vegetation may increase moose sightability and increase vulnerability in a low prey-density system. In line with studies that demonstrate selection for prey density (McPhee et al., 2012b), wolves may select riparian corridors because moose utilize them in the winter (Baigas et al., 2010; MacCracken et al., 1997). Moose density and distribution data spanning the entire study period were not available. Within the forested habitat classes, burns may play an important role in moose and wolf movement. However, burn perimeter data encompass unburned areas and often fire intensity is not well accounted for (Kasischke et al., 2010). The response of moose and wolves to burn age could be dependent on any of those factors.

Messier and Crête (1985) surmised that 0.20 moose/km² was the lowest density for which wolves could survive. Within our system (<0.20 moose/km²), wolves are clearly surviving and were making longer movements to do so. In order to survive in a low prey-density system, wolves within the Yukon Flats have adapted. Wolf territories are likely to be large due to low prey-densities (Kittle et al., 2015; Lake et al., 2015). Wolves on the Yukon Flats exhibited territories among the largest and densities among the lowest reported in North America (Lake et al., 2015). Our analysis presents a mechanism for why territories are so large and densities low in systems of low prey biomass. As wolves travel longer distances in response to low availability of vulnerable prey, territory size area inflates. Wolf densities likely decrease as territories overlap due to inter-pack strife. Hence, long search distances contribute to low wolf densities in systems of low prey availability.

A key result of our study of movement in a low prey-density system was that wolves move farther to find prey. As such, our results could be extended to any low prey-density system and may be particularly poignant in areas where density changes from high to low prey. Managers in regions with wolf-prey relations could consider the impact of wolves on decreasing ungulate density. As an example, if deer herd numbers decline, or deer became less vulnerable, managers may expect wolf pack territories to enlarge and wolf pack densities to decline. Managers within systems of small-bodied ungulates would need to define the minimum prey density necessary to sustain wolves as it is unlikely that wolves would persist at <0.20 deer/km² due to the relatively small body size of deer compared to moose. Knowing that wolf territories would expand as prey densities decrease would aid in modeling wolf impact on declining deer populations.

Broadly, our results offer insight into movements of a coursing predator in a low-density, single-prey system, and a mechanism for maintaining a kill rate. The plastic (i.e., extendable) nature of wolf movement suggests they can adjust accordingly to accommodate for prey densities even below the 0.20 moose/km² threshold proffered by Messier & Crête (1985). Current low prey densities on the Yukon Flats have remained stable since documentation began more than fifty years ago (Bentley, 1961; Gasaway et al., 1992; Lake, 2013). However, if prey-density or vulnerability were to further decline, we hypothesize that wolves may further adjust travel distances to locate vulnerable prey. This may continue to a point until the number of days between kills becomes limiting. At such a point, wolves may starve, optimize pack size (i.e., small packs) or disperse to find suitable prey availability. Thus, wolf persistence in our study area appears to be limited by the number of days between kills, which is a function of effort, primarily distance traveled to locate a vulnerable prey. As wolves and moose have occurred on the Yukon Flats at low density for at least decades (Gasaway et al., 1992), it does not seem that travel distance or the number of days between kills have been limiting.

2.7 References

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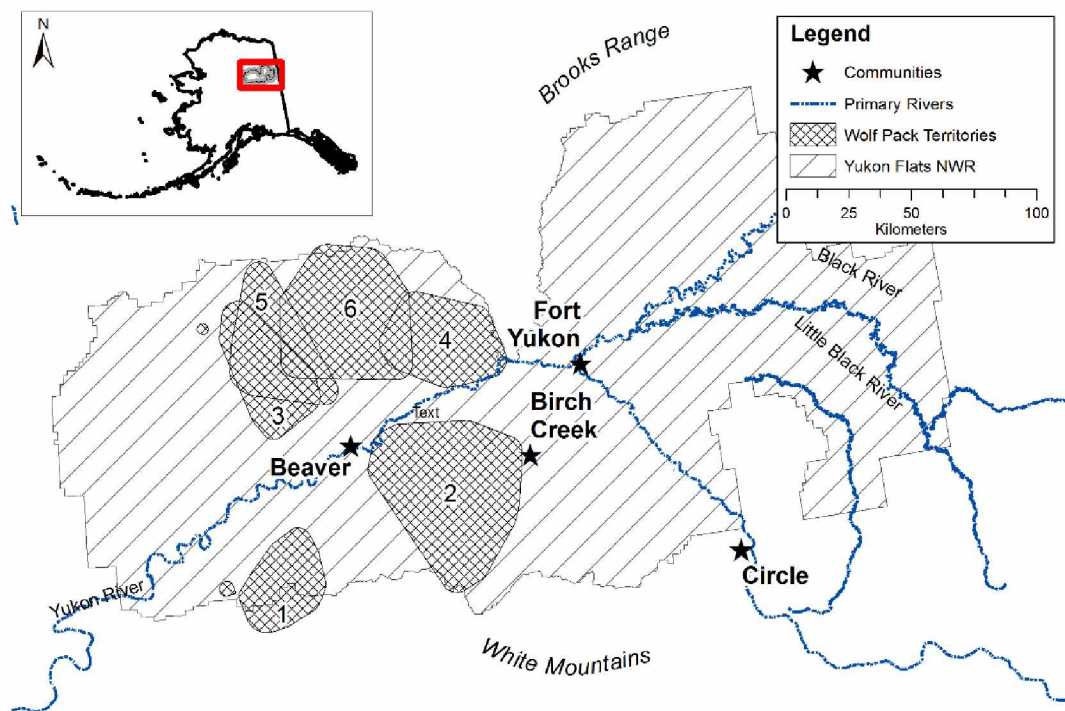


Figure 2-1: Study area including the boundary of the Yukon Flats National Wildlife Refuge and the minimum convex polygon boundaries of the six wolf packs analyzed. Pack territories are labeled by number. Lost Creek Pack (1), Beaver Creek Pack (2), Hodzana Mouth Pack (3), Crazy Slough Pack (4), Hodzana Pack (5), and Bald Knob Pack (6)

Table 2-1: Summary of covariates utilized in resource selection function (RSF) analysis. The response was binary. If the location was a wolf use point it was coded “1”, and if the location was generated randomly it was coded “0”. Categorical variables were grouped together as: NLCD₁ (11 – water), NLCD₂ (31 – Barren, 52 – Shrub Scrub, 51 – Dwarf Scrub), NLCD₃ (41 – Deciduous Forest, 42 – Evergreen Forest, 43 – Mixed Forest), NLCD₄ (72 – Sedge/ Herbaceous Wetlands, 90 – Wood Wetlands, 95 – Emergent Wetlands). The group description describes the continuous and categorical variables, and GIS layer derived from describes the data surface or derived data surface.

Groups	Binned	Group Description	GIS Layer Derived From
Continuous	--	Minimum distance to waterbodies or rivers	National Hydrography Dataset
Continuous	--	Linear distance from ridge lines	Ridgeline analysis from 17m ASTER data
11	1	Open Water	National Land Cover Dataset 2001
31,52, 51	2	Barren/ ShrubScrub/Dwarf Scrub	National Land Cover Dataset 2001
41, 42,43	3	Deciduous Forest, Evergreen Forest, Mixed Forest	National Land Cover Dataset 2001
72,90,95	4	Sedge/Herbaceous, Woody Wetlands, Emergent Wetlands	National Land Cover Dataset 2001

Table 2-2: Results of wolf behavior based on kill path characterization for wolves on the Yukon Flats, Alaska, 2009-2010. If data were not normally distributed, we report the mean, and median of the results.

Pack	Number in Pack	Data Start	Data End	Number of Locations	Mean Handling Time (days) (sd)	Mean Travel Speed (km/hr) (median)	Mean Days Between Kills (median)	Mean Travel Distance (km)
Bald Knob	4	12/21/09	4/7/10	832	4.4 (2.1)	0.7 (0.4)	5.7 (4.1)	69.4
Beaver Creek	8	11/7/09	3/31/10	1123	3.0 (1.57)	0.7 (0.3)	4.3 (2.5)	58.1
Crazy Slough	4	11/10/09	3/27/10	1024	5.0 (2.7)	0.6 (0.5)	7.2 (5.4)	84.8
Hodzana	5	11/9/09	3/20/10	1031	3.7 (1.7)	0.6 (0.3)	5.3 (4.7)	55.0
Hodzana Mouth	5	11/13/09	1/17/10	499	7.7 (5.0)	0.7 (0.5)	5.3 (6.9)	76.4
Lost Creek	2	11/15/09	3/29/10	1052	3.1 (1.0)	0.5 (0.4)	8.6 (8.75)	70.7
All Packs	--	--	--	5561	4.0 (2.5)	0.6 (0.36)	5.9 (5.6)	65.2

Table 2-3 : Pearson's Chi-square contingency table examining differences in observed and expected habitat classes of wolf locations. Expected use assumes a random distribution of points, and was calculated as percent area * n of use points. Our results show preliminarily differences in use and expected use.

Location of Points	Percentage of Area	Use Points	Expected Use
NLCD 1	3.6%	135	86
NLCD 2	23.2%	58	553
NLCD 3	62.1%	2024	1482
NLCD 4	11.1%	168	264
Totals	100.0%	2385	2385
Pearson ChiSquare:		317.86	
P-Value		<0.0001	

Table 2-4: Results of model selection of generalized linear mixed-effects resource selection models for wolves. All models included a random pack intercept. Sample sizes of use and available points were constant for each model (n use = 2,385, n available = 5,461). We report model structure, number of parameters (k), log likelihood (LL), and AIC corrected for small sample sizes (AIC_c).

Model Name	Structure	LL	ΔAIC _c
Global	use.corrected ~ nlcd + dist.water.all.s + dist.ridge.s + (1 ID)	-4192.9	0
m3	use.corrected ~ nlcd + dist.ridge.s + (1 ID)	-4215.1	42.2
m4	use.corrected ~ nlcd + (1 ID)	-4327.7	267.5
m5	use.corrected ~ dist.water.s + (1 ID)	-4342.9	296
m2	use.corrected ~ nlcd + dist.water.all.s + (1 ID)	-4778.6	1163.3
m1	use.corrected ~ dist.ridge.s + (1 ID)	-4780.8	1167.8

Table 2-5: Coefficient output for best-fit generalized linear mixed-effects model. The model formula was (use ~ NLCD_(4 levels, cat.) + Distance Water_(scaled, cont.) + Distance Ridges_(scaled, cont.) + (1 | ID)_(random intercept)). The p-value (Pr(>|z|)), was not significant for NLCD₃, and although is not significant for NLCD₁, it is not interpretable for the intercept.

	Estimate	z-value	Std. Error	z-value	Pr(> z)
NLCD ₁ (Intercept)	-0.3769		0.1593	-2.365	0.018
NLCD ₂	-2.9609		0.1896	-15.614	<0.0001
NLCD ₃	0.1437		0.1304	-1.102	0.27
NLCD ₄	-0.737		0.1529	-4.82	<0.0001
Distance Water _{scaled}	-0.5161		0.0344	-14.99	<0.0002
Distance Ridges _{scaled}	-0.14628		0.0273	-5.359	<0.0003

Table 2-6: Activity budget of wolves based on path characterization as percentage of time spent at each behavior from our path characterization.

Pack	Kill Cluster	Resting	Revisit	Traveling
Bald Knob	46.0%	6.5%	7.8%	39.7%
Beaver Creek	41.9%	1.0%	0.2%	48.2%
Crazy Slough	43.8%	7.5%	8.2%	40.5%
Hodzana	43.1%	9.7%	3.5%	43.7%
Hodzana Mouth	59.5%	12.8%	1.2%	26.5%
Lost Creek	28.2%	7.8%	19.7%	44.3%
Mean	43.7%	7.6%	6.8%	40.5%

Table 2-7: Published wolf movement characteristics. We list the results of this study in the first row, and provide context for each study by including the season, geographic region, and prey species of each.

Author	Predation Mechanism	Study Type	Interval (hours)	Geographic Region	Season	Prey Species *	Prey Density / km ²	Wolf Density per 1000km	Average Time to Event (days)	Average Search Distance	Handling Time (Days)	Mean Search Speed (km/hr)
Results of Johnson et al. 2015	Search to Kill	GPS	3	Alaska	Winter	M	0.2	2-3	5.9	65.2	4.0	0.6
Vander Vennen 2014	Search to kill	GPS	2.5	Northern Ontario	Winter	M	--	--	--	--	--	0.2 – 0.7
McPhee, Webb & Merrill 2012b	Search to Kill	GPS	2	Rocky Mountains, Alberta	Winter	E,M,WH	0.28, 0.24, 0.10	12.4	5.3 ± 0.77	--	--	--
Hayes et al. 2000	Kill Rate	Radio Telemetry	--	East-Central Yukon	--	M	0.339 0.61	--	--	--	2.9 ± 0.16	--
Sand et al. 2005	Kill Rate	GPS	1	South Sweden, Southeast Norway	Winter	M	1.1 ± 0.1	--	3.6 – 4.0	--	1.25	--
Merrill & David Mech 2000	Full Travel Path	GPS	3	Northern Minnesota	Winter	--	--	--	--	--	--	3.55
Moffatt 2012	Search to Kill	GPS	5	Northern Ontario	Winter	M, WC	kriged surface	5.2 – 7.8	3.0	27.4	6.0	--
Moffatt 2012	Revisits	GPS	5	Northern Ontario	Winter	M, WC	kriged surface	5.2 – 7.8	4.125	38.8	1.2	--
Gurarie et al. 2011	Hunting	GPS	0.5	Finland	Summer	M, R	--	--	--	--	--	mean = 1.21 max = 6.25
Mech & Cluff 2011	All Movement	GPS	12	Nunavut, Canada	Winter	--	--	--	--	--	--	1.7
Eriksen et al. 2011	All Movement	GPS	4	Southeastern Norway	Summer, Autumn	M	1.3 – 1.7	--	--	--	--	0.18
Eriksen et al. 2003	Kill Rate	GPS	1	Scandinavian peninsula, Norway, Sweden	Winter	M,D	1.08, 0.9	--	4.1 - 5.1	--	1.2 ± 1.1	--
Zimmermann et al. 2007	Kill Rate	Kill Rate	0.5 - 1	Scandinavian peninsula, Gafjell, Borgrangen territories	Winter	M	1.2 - 2.6	--	--	--	0.04 - 2.4	--
Musiani, Okarma and Jedrzejewski 1998	Movement	Radio Telemetry	2	Poland	Winter	M	--	--	--	--	--	3.8
Mech 1994	Movement	Observation	--	Nunavut, Canada	Summer	--	--	--	--	--	--	8.7
McPhee, Webb & Merrill 2012b	Search to Kill	GPS	2	Rocky Mountains, Canada	Winter	M	0.61	12.4	4.9 ± 0.56	--	--	--
Jedrzejewski et al. 2001	--	Radio Telemetry	0.25 - 0.50	Poland	All	D, WB, EB, M	--	0.002 - 0.003	--	--	--	2.36 +- 0.12

* M = Moose, WC = Woodland Caribou, D = Deer, WH = Wild Horse, E = Elk, R = Reindeer, WB = Wild Boar, EB = European Bison

Chapter 3 Conclusion

Within the Yukon Flats, competition between humans and predators is an important interaction for game managers because subsistence communities in the Yukon Flats utilize moose (*Alces alces*) as a primary resource (78% of households) and wolves (*Canis lupus*) hunt them as an obligatory prey item. Moose are scarce and have been held at a low-density equilibrium since surveys began over 50 years ago (Bentley, 1961; Gasaway et al., 1992; Lake, 2013). Quantifying the amount of direct competition is difficult because of the complexities introduced by a large study area, uncertain movement behavior of moose, a dynamic interaction of humans and their environment and a multi-predator system. Combined predation from bears (*Ursus americanus*, *U. arctos*), wolves, legal harvest of bulls, and illegal harvest of cows (Bertram & Vivion, 2002) all contribute to the low density of moose in the Yukon Flats.

Our study was the first to quantify moose hunter access in rural Alaska. We demonstrated concentration around primary, navigable waters. Within the Yukon Flats, our approach may supplement estimates of subsistence moose harvest based on harvest ticket reporting, which is unreliable in that region. Managers may use our results of access to alleviate competition from non-local hunters by directing them outside of likely subsistence access areas. Extending our model to other hunting systems, our approach to modeling hunter access may provide managers with an alternative approach to estimating human harvest of moose or other game animals where access is a strong component of harvest success. Depending on management goals, managers could use our model to forecast the effect of new access (e.g., a

new road) on game populations to understand the impacts before harvest information is available.

Our study was the first to quantify wolf movements in a low prey-density system. Compared to high-density systems, wolves within the Yukon Flats were traveling farther to kill moose and are selecting for river corridors that likely enable efficient travel and may increase their likelihood of encountering prey. Our findings of long travel distances explain why wolf territories become larger within low prey-densities (Kittle et al., 2015; Lake, Caikoski, & Bertram, 2015). Since wolf travel distance to kills could continue to extend if prey densities decrease, it is plausible that wolves can exist at moose densities even less than the currently observed low densities (<0.20 moose/km²). Managers in systems of high prey-density could expect wolf territories to grow if prey densities decrease.

We can evaluate competition with humans by assuming that selection for travel corridors by packs within territories that overlap navigable water would increase their chance of competition with humans for moose. Our findings in Chapter 1 and Chapter 2 created an opportunity to quantify competition between humans and wolves for moose by evaluating their spatial overlap. Managers within this system may consider humans to be explicitly linked to their environment, and hence, an evaluation of humans, wolves, and moose as a social-ecological system is appropriate. Often, research questions pertaining to management in a SES acknowledge their social context. In the context of the SES framework, our research model quantifies human use of the landscape and wolf movement patterns to inform management of the potential for competition between wolves and humans. On average subsistence hunters

travel 47 km (SD = 32 km) upriver and 0.9 km (SD = 0.6 km) from rivers to harvest moose. Wolf selection decreased as distance from rivers increased. The likelihood of competition along navigable waters was illustrated by overlaying locations of the Beaver Creek pack (Figure 3-1) on our human access model. Of those, 75% of the locations fell within likely hunter access areas (Table 3-1), whereas 287 (26%) points did not fall inside of the human access area.

There was likely spatial overlap between moose hunters and wolves because they use the same functional predation technique; wolves and subsistence moose hunters are each coursing predators. To understand humans as a coursing predator, it is important to put their movements in social context. Subsistence hunters utilize traditional use areas (Caulfield, 1984; Stevens & Maracle, 2012). In some cases, our results from Chapter 1 demonstrate Fort Yukon users traveling >200 km (actual river distance) to the east to traditional use areas. Along their journey, they may opportunistically take moose (Stevens & Maracle, 2012). If humans are not traveling to distant traditional use areas they often focus on river hunts and drive along rivers in search of bull moose. In effect, humans are concentrating their efforts in areas where prey are likely to be found. By using the same predation strategy (coursing) as wolves, they compete by default.

Our modeling efforts create opportunities for more rigorous spatial evaluations of competition between humans and predators for a common prey resource. Such an analysis would require a careful integration of biological and social datasets. It is critical that future studies evaluating competition between humans and wolves collect datasets that temporally overlap; predator-use datasets would need to spatially overlap moose harvest by humans

during the autumn. This is important, as it is likely that wolf behavior and habitat selection differ in the summer (Metz, Vucetich, Smith, Stahler, & Peterson, 2011; Zimmermann, Wabakken, Sand, Pedersen, & Liberg, 2007) due to changes in moose distribution, presence of alternative prey such as salmon and waterfowl, and lack of frozen river corridors. A future study could consider indirect competition by measuring moose movement, to estimate effect of predator-killed moose away from navigable waters on human harvest.

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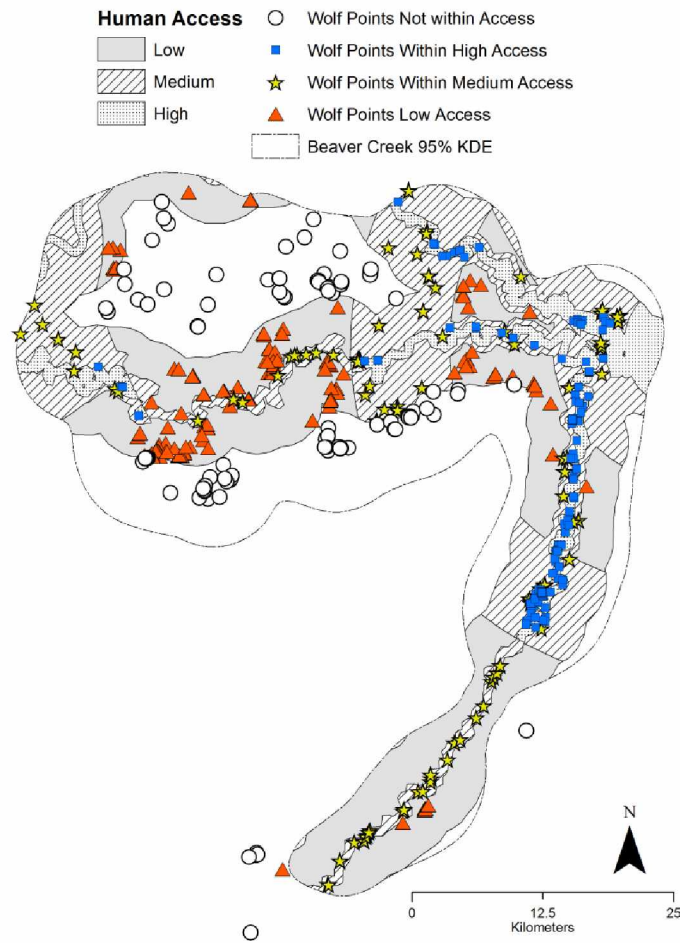


Figure 3-1: Spatial overlap in wolf travel and kill cluster points with human access calculated in Chapter 1. An index of “high” indicates that humans were likely to use that region to hunt moose. Ordinarily, low is the least likely. Only 26% of points within the Beaver Creek pack do not overlap with human use areas.

Table 3-1: Summary of Beaver Creek wolf locations from 11/11/2009 - 03/23/2010. Locations were deemed at a kill site, or traveling from the results of our path characterization. We determined whether the points were present within human high access (1), medium access (2), or low access (3) areas. Only 26% of points did not overlap with human access.

	Access Index				
	1	2	3	None	Total
Kill	132	47	131	139	449
Traveling	197	158	168	148	671
Total	329	205	299	287	1120
Percentage	29%	18%	27%	26%	100%

Appendix Email approval from non-committee co-authors



Kelda Britton

12:01 PM

RE: Manuscript Use Approval

To: Ian Johnson; Kelda Britton

Hi Ian,

You have my approval for the first chapter to use in the manuscript.

I really enjoyed your thesis presentation. Let me know if you have an extra copy that I can share with our staff.

Many thanks,

Kelda

From: Ian Johnson [mailto:johnsoni@live.com]

Sent: Tuesday, November 17, 2015 11:55 AM

To: Kelda Britton

Subject: Manuscript Use Approval

Importance: High

Hi Kelda,

I am finalizing my thesis to the Dean. I need your approval as a co-author on my first chapter to use it in the Manuscript.

This is a last minute detail, if you could please respond yay or nay today that would be great.

Thanks!!

Ian

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James Kelly

12:19 PM

Re: Manuscript Use Approval

To: [Ian Johnson](#)

Yes....

James

On Tue, Nov 17, 2015 at 11:57 AM, Ian Johnson <johnsoni@live.com> wrote:

Hi James,

I am finalizing my thesis to the Dean. I need your approval as a co-author on my first chapter to use it in the Manuscript.

This is a last minute detail, if you could please respond yay or nay today that would be great.

Thanks!!

Ian

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